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L system strategy: the associated growth of a characteristic type of multicellular development

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A typical mode of development is frequently observed at all levels of organization in the lower and higher plants: a zone of undifferentiated cells with great mitotic activity and generating a zone of differentiated cells which have lost all ability to divide. A question is put: does this type of development imply, by its very nature, a specific form of growth curve for organisms, organs, or parts of organs, which exhibit this development? To answer a question formulated in such a general manner causes difficulties of a biological nature, so it is proposed to represent simply this type of development in a one-dimensional array of cells by a primitive model assumed to summarize the root of the developmental mode. The model, consisting of a class of L systems, enables a specific form of growth curve to be found and suggests a connection between a frequently occurring type of development and a form of growth curve often encountered (growth by successive ' platforms '). The value of the strategy used is to show that very simple mechanisms may exist which can, by themselves, explain some phenomena (in particular, periodic phenomena) observed at a high level of organization.

1. Introduction

Lindenmayer systems, or L systems, which are today one of the most widely investigated areas of formal language theory, were introduced by Lindemayer (1968) as a model for the developmental growth in filamentous organisms. A one-dimensional array of cells, defining the organism at a given moment, is symbolized by a sequence of letters (or filament). The letter which is assigned to each cell is regarded as a discrete cellular state at this moment; each cell may be in one of a finite number of states (distinct letters).

" The justification for assuming a finite set of states is that there are usually threshold values for parameters that determine the behaviour of a cell. Thus, with respect to each of these parameters, it is sufficient to specify two conditions of the cell: ' below threshold ' and ' above threshold ', although the parameter itself may have infinitely many values" (after Herman).

An L system consists of a finite set of letters (alphabet), of a set of rewriting rules (productions), of an initial sequence of letters (axiom) and of an environmental letter corresponding to the influence of the environment. The axiom, or starting filament, symbolizes the organism at an arbitrary moment of origin; time is assumed to progress in discrete steps. The subsequent stages of development of the initial filament are symbolized by consecutive sequences of letters which are obtained, starting from the origin time, by rewriting all the letters of a sequence, simultaneously at each time step. Rewriting rules take into account cell division, since any single letter may be rewritten as two letters. When the

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rewriting of a letter depends on the m letters to its left and the n letters to its right in the sequence, we use the term a ' context-dependent ' L system, denoted by $(m, n)L$ *system*; if $m = n = 0$, we use the term a ' context-independent ' L system ((0, 0)L system or 0L system). An (m, n)L system is *deterministic*, denoted by $D(m, n)L$ *system*, when each letter can be rewritten in only one way in each context. All systems considered in this paper are deterministic. The reader specially concerned with biological aspects of L systems is referred to the works of Baker and Herman (1972 a, b), Frijters and Lindenmayer (1974), Hellendoorn and Lindenmayer (1974), Herman (1971, 1972), Herman and Schiff (1974), Lindenmayer (1968, 1971, 1975), Lück (1975), Lück and Lück (1976), and Mayoh (1974). More generally, for a survey of L systems from both theoretical and biological points of view, the reader will find very complete information in the book by Herman and Rozenberg (1975), in that of Rozenberg and Salomaa (1974) and in that of Lindenmayer, and Rozenberg (1976).

A particularly interesting topic in the study of L systems is the theory of *growth functions*, functions which give the length (number of letters) of a filament at each stage of its development. Papers treating the topic of growth functions of D0L systems are Doucet (1973), Paz and Salomaa (1973), Salomaa (1973), Szilard (1971), and Vitányi (1973). Growth functions of $D(m, n)$L systems are considered by Karhumäiki (1974 a, b) and Vitányi (1974). A survey paper in the field of growth functions is by Herman and Vitányi (1976).

In this paper, we are interested in a typical mode of development frequently observed at all levels of organization in the lower and higher plants: a zone of undifferentiated cells with great mitotic activity and generating a zone of differentiated cells which have lost all ability to divide. More precisely, we put the following question: does this type of development imply, by its very nature, a specific form of growth curve for organisms, organs or parts of organs, which exhibit this development? Of course, to answer a question formulated in such a general manner causes difficulties of a biological nature because it entails, among other things, the detailed knowledge of the underlying mechanisms of this type of development, mechanisms which are very specific in each particular case, and also which should be sufficiently general to be useful for characterizing a general type of development. So we have to restrict our ambitions and only consider the possibility of the existence of simple and general mechanisms which are able to explain, by themselves, such phenomenology. Thus our approach here is to represent what is most characteristic and most essential in the considered typical development by a basic model, as simple as possible, where the developing organism or organ is composed of a one-dimensional array of cells. This model will be formally a class of L systems defined by a number of developing properties and supposed to summarize the essentials of this development. In what follows we shall show that, for this class of L systems, the mentioned type of development implies a specific form of the associated growth function.

2. Formal definition of D(*m*, *n*)L systems

2.1 *Generalities on finite sequences*

Let A be a finite set. For all integers n (positive or equal to 0), we denote by A^n the set of all sequences of length n with all their terms belonging to A. In particular, $A^1 = A$ (any sequence of length 1 is denoted as its unique term) and A^0 is the set with only one element, which is denoted by e, and called the empty sequence. We denote by A^* the set of all finite sequences, and by A^+ the set of all finite non-empty sequences: $A^* = \bigcup_{n\geqslant 0} A^n$ and $A^+ = \bigcup_{n\geqslant 1} A^n$. For each element z of A^*, we denote its length by $|z|$ (thus, we get $|e| = 0$ and $z \in A^{|z|}$).

Given a sequence z of length n, let us say $z = (a_1 \ldots a_n)$, and two integers l and l' such that $0 \leqslant l \leqslant l' \leqslant n$, we call the *section of z delimited by l and l'* (denoted by $T(z, l, l')$) the sequence of length $l'-l$, $(b_1 \ldots b_{l'-l})$, defined by: for all i, such that $1 \leqslant i \leqslant l'-l$, $b_i = a_{l+i}$ (i.e. $(b_1 \ldots b_{l'-l}) = (a_{l+1} \ldots a_{l'})$). In particular, we have:

for any l such that $0 \leqslant l \leqslant n$, $T(z, l, l) = e$;

if $|n| \geqslant 1$, then, for any l such that $1 \leqslant l \leqslant n$, $T(z, l-1, l) = a_l$;

$T(z, 0, n) = z$.

Subsequently, it will be convenient to adopt the following notations: $\hat{A}^*$ is the set of all triplets (z, l, l') where z belongs to A^* and l and l' are two integers satisfying $0 \leqslant l \leqslant l' \leqslant |z|$; $\hat{A}^+$ is the set of all triplets (z, l, l') where z belongs to A^+ and l and l' are two integers satisfying $0 \leqslant l < l' \leqslant |z|$. We note that T is a mapping from $\hat{A}^*$ to A^*, and moreover, that for any element (z, l, l') of $\hat{A}^+$, $T(z, l, l')$ belongs to A^+.

We define on A^* a binary operation called *concatenation* (in other words, 'placing end to end') in the following way: to each pair (z_1, z_2) of finite sequences, we assign the unique finite sequence, denoted by z_1z_2, which satisfies:

$|z_1z_2| = |z_1| + |z_2|$;

$T(z_1z_2, 0, |z_1|) = z_1$;

$T(z_1z_2, |z_1|, |z_1| + |z_2|) = z_2$.

This operation is obviously associative, and admits e as its unit element. Let p finite sequences, $z_1, z_2, \ldots, z_p$, be given; their product (with respect to concatenation) is denoted by $z_1z_2 \ldots z_p$, or $\prod_{1\leqslant i\leqslant p} z_i$. If all sequences $z_1, z_2, \ldots, z_p$ are equal to the same sequence v, we denote $\prod_{1\leqslant i\leqslant p} z_i = v^p$ (this is the pth power with respect to concatenation of v). Furthermore, we put $v^0 = e$, and note that, for all p, $v^{p+1} = v^pv$. If z is a finite sequence, and $(l_0, \ldots, l_p)$ is an increasing sequence of integers, with 0 and $|z|$ for its extreme terms (i.e. $0 = l_0 \leqslant l_1 \leqslant \ldots \leqslant l_p = |z|$), then we get $z = \prod_{1\leqslant i\leqslant p} T(z, l_{i-1}, l_i)$; in particular, any sequence is obtained by concatenation of its terms (we have $(a_1 \ldots a_n) = \prod_{1\leqslant i\leqslant p} a_i$). Hence, if h is an element of A, h^p is the sequence of length p with all its terms equal to h (in the particular case where $p = 0$, we find again $h^0 = e$).

2.2. $D(m, n)L$ *systems*

Let m and n be two integers (positive or equal to 0). We call $\mathrm{D}(m,n)\mathrm{L}$ system every quadruplet $S = \langle A, \delta, g, x_0\rangle$, where:

A is a finite set, called an *alphabet* (its elements are called *letters*, and the elements of A^* are called *filaments*);

g is an element of A, called the *environmental letter*;

x_0 is an element of A^+, called the *axiom*;

δ is a mapping from A^{m+1+n} to A^*, called the *rewriting rule* (for any element y of A^{m+1+n}, let $y=(a_1 \ldots a_m a_{m+1} a_{m+2} \ldots a_{m+1+n})$, we shall state that '$\delta(y)$ is the rewriting of a_{m+1}, depending on the context $a_1 \ldots a_m$ to its left and on the context $a_{m+2} \ldots a_{m+1+n}$ to its right ').

To each filament w of length k we assign its *extension*, denoted by $\bar{w}$, and defined by $\bar{w}=g^m w g^n$. Then we can assign, to the D(m,n)L system $\langle A, \delta, g, x_0\rangle$, a mapping from A^* to itself, called the *generating function*, denoted by δ', and defined by:

$\delta'(e)=e$;

if w is an element of A^+, $\delta'(w)= \prod_{1 \leqslant i \leqslant |w|} \delta(T(\bar{w}, i-1, m+i+n))$

The preceding formula has the following interpretation; for any non-empty w, $\delta'(w)$ is obtained by *concatenation of the rewritings* of the successive terms of w, the context of each term being composed:

to its left, of the m terms which precede it in w (completed on the left, if need be, with as many g as is necessary);

to its right, of the n terms which succeed it in w (completed on the right, if need be, with as many g as is necessary).

δ' interprets the development of a whole filament during a time step. The letters g added to the right and to the left of w represent implicitly the influence of a constant environment upon the organism symbolized by w. Given an integer $i \geqslant 0$, we denote by $(\delta')^i$ the ith power (with respect to the composition of the mappings) of δ'; for any filament w, we have $(\delta')^0(w)=w$, and for any integer $i \geqslant 0$, $(\delta')^{i+1}(w)=\delta'((\delta')^i(w))$.

We call the *language produced by S*, denoted by $L(S)$, the infinite sequence with $(\delta')^i(x_0)$ for its general term; $L(S)$ represents, in point of fact, the subsequent stages of development, during the successive time steps i, of a filament symbolized at the initial time (0) by the axiom x_0.

We call the *growth function associated with S*, denoted by f_S, the mapping from the set of positive or null integers to itself, which, at each i, assigns the length of $(\delta')^i(x_0)$: $f_S(i)=|(\delta')^i(x_0)|$.

A D(m,n)L system is called *propagating* (denoted by PD(m,n)L system) if and only if, for any element v of A^{m+1+n}, $\delta(v)$ is non-empty. It is clear that the growth function of a PD(m,n)L system is increasing (if $i \leqslant i'$, $f_S(i) \leqslant f_S(i')$).

Subsequently we shall consider only PD(m,n)L systems and we shall write x_i for $(\delta')^i(x_0)$.

2.3. *Descendance*

For any filament w of length k, and any i such that $1 \leqslant i \leqslant k$, let $N(w,i) = |\delta(T(\bar{w}, i-1, m+i+n))|$; this is the length of the section of $\delta'(w)$ ' descending ' from the ith term of w; obviously, we have the equality $|\delta'(w)| = \sum_{1 \leqslant i \leqslant k} N(w,i)$.

$\hat{A}^+$ being (as in § 2.1.) the set of all triplets (w, l, l') such that w is a non-empty filament, and l and l' are two integers satisfying $0 \leqslant l < l' \leqslant |w|$, we define a mapping, denoted by $\hat{\delta}$, from $\hat{A}^+$ to itself as

$$\hat{\delta}(w,l,l') = \left(\delta'(w), \sum_{i \leqslant l} N(w,i), \sum_{i \leqslant l'} N(w,i) \right)$$

$\sum_{i\leqslant l} N(w,i)$ and $\sum_{i\leqslant l'} N(w,i)$ are the integers which delimit, in $\delta'(w)$, the section 'descending' from the section of w delimited by l and l'; this last property is expressed by the formula

$$T(\hat{\delta}(w,l,l')) = \prod_{l+1\leqslant i\leqslant l'} \delta(T(\bar{w}, i-1, m+i+n))$$

In particular, we have $\hat{\delta}(w,i-1,i) = (\delta'(w), \sum_{j<i} N(w,j), \sum_{j\leqslant i} N(w,j))$, and $\hat{\delta}(w,0,|w|) = (\delta'(w), 0, |\delta'(w)|)$. For all positive or null integers p, $\hat{\delta}^p$ denotes the pth power (with respect to the composition of mappings from $\hat{A}^+$ to itself) of $\hat{\delta}$; i.e. for any element (w,l,l') of $\hat{A}^+$, we have $\hat{\delta}^0(w,l,l') = (w,l,l')$ and, for all p, $\hat{\delta}^{p+1}(w,l,l') = \hat{\delta}^p(\hat{\delta}(w,l,l'))$.

We define a mapping, denoted by γ_p, from $\hat{A}^+$ to A^+, by: $\gamma_p(w,l,l') = T(\hat{\delta}^p(w,l,l'))$. γ_p is called the *descendance of order p* (actually, $\gamma_p(w,l,l')$ is the section of $(\delta')^p(w)$ descending from the section of w delimited by l and l'). In particular, we have $\gamma_0 = T$, and for all p, $\gamma_p(w,0,|w|) = (\delta')^p(w)$. We note that, given l and l', if $(l_0,\ldots,l_s)$ is a strictly increasing sequence of integers, with l and l' for its extreme terms, we obtain $\gamma_p(w,l,l') = \prod_{1\leqslant i\leqslant s} \gamma_p(w, l_{i-1}, l_i)$; this last formula means that if a section of w is itself divided into s successive 'sub-sections', then the descendance of order p of this section is obtained by concatenation of the descendances of order p of these sub-sections. This obvious property will be subsequently referred to as *decomposability of descendances*; in particular, we have, if $l=0$ and $l'=|w|$, $(\delta')^p(w) = \prod_{1\leqslant i\leqslant s} \gamma_p(w, l_{i-1}, l_i)$.

3. A special class of PD(m,n)L systems

We shall try to draw conclusions about the general form of the growth function of a one-dimensional array of cells, bathed in a constant environment, and showing the following characteristic type of development: whatever the considered stage of development of this array may be, all the cells of which it is composed, except the one lying on the far right-hand side (apical), will have respectively, after a more or less long lapse of time, a descendance composed of cells all having eventually reached the same stationary state (denoted by h), a state for which all division is impossible. This lapse of time may be zero if the cell considered is already in the state h; furthermore, the growth of the array is infinite. In order to give a more concrete idea of this situation, let us say that it concerns a cellular array which looks like a generating layer of cells (where the apical cell is never in the state h) behind which cells, all having eventually reached a stationary state h (for instance, an irreversible state of differentiation), continually accumulate. In a formal way, we are interested in the general form of growth of cellular arrays, answering by hypothesis conditions of application of PD(m,n)L systems, and such that it is possible to find, for each of them, m, n, A, δ, g, x_0, such that $S = \langle A, \delta, g, x_0\rangle$ satisfies the following properties.

(P 1) *Properties dealing uniquely with* δ

(P 1.1) *Maximum divisibility into two parts*
For any y belonging to A^{m+1+n}, $|\delta(y)|$ is equal to 1 or 2.

(P 1.2) *Existence of a stationary state*
There exists an element of A, denoted by h, such that, for any z belonging to A^m, and for any z' belonging to A^n, we have : $\delta(zhz')=h$ (h is called the *stationary state*, and any filament with all its terms equal to h is said to be a *stationary filament*).

(P 2) *Properties bringing in the axiom* x_0

(P 2.1) *Infinite growth*
$f_S(i)$ tends to $+\infty$ when i tends to $+\infty$.

(P 2.2) *Stationary outcome of the non-apical section*
For any integer i, positive or equal to zero, there exists an integer p, positive or equal to zero, such that the descendance of order p of the section of $x_i(\in L(S))$ delimited by 0 and $|x_i|-1$ (i.e. of the whole x_i deprived of its last cell, called the *apical cell*) is stationary.

Systems S which possess the properties (P 1) and (P 2) will be called S_a systems.

3.1. *First consequences*

3.1.1. *Remarks about the property* (P 2.2) : *stationary outcome*

For any positive or null integer i, let us denote by p_i the smallest integer such that $\gamma_{p_i}(x_i, 0, |x_i|-1)$ is stationary and by q_i the length of $\gamma_{p_i}(x_i, 0, |x_i|-1)$; then we obtain, under the property of stationarity of h (property (P 1.2)), for all i' greater than or equal to p_i, $\gamma_{i'}(x_i, 0, |x_i|-1)=h^{q_i}$ (let us remark that, if $T(x_i, 0, |x_i|-1)$ is already itself stationary, we have $p_i=0$).

It is obvious that, if l and l' satisfy $0\leqslant l<l'\leqslant |x_i|-1$, the descendance of a sufficiently high order of $T(x_i, l, l')$ will be stationary. Conversely, let $(l_0, \ldots, l_s)$ be a strictly increasing sequence of integers, with 0 and $|x_i|-1$ for its extreme terms ; let us suppose that, for any j $(1\leqslant j\leqslant s)$, the descendance of $T(x_i, l_{j-1}, l_j)$ is, for a sufficiently high order, stationary ; then, it follows from the property of decomposability of descendances that the descendance of $T(x_i, 0, |x_i|-1)$ itself, is for a sufficiently high order, stationary. This sufficient condition for stationarity of a descendance of sufficiently high order of $T(x_i, 0, |x_i|-1)$ will be, in particular, employed with $s=|x_i|-1$: in this case, we have to consider all sections of x_i made up of only one element. If, for all j, we denote by p_{ij} the smallest integer such that $\gamma_{p_{ij}}(x_i, j-1, j)$ is stationary, and by q_{ij} the length of $\gamma_{p_{ij}}(x_i, j-1, j)$, we obtain the following obvious properties :

for all $i'\geqslant p_{ij}$, $\gamma_{i'}(x_i, j-1, j)=h^{q_{ij}}$;

$p_i=\sup(p_{i1}, \ldots, p_{i,|x_i|-1})$;

$$q_i=\sum_{1\leqslant j\leqslant |x_i|-1} q_{ij}.$$

3.1.2. *The apical cell divides an infinite number of times*

Let I be the set of positive or null integers i such that $N(x_i, |x_i|)=2$ (using the notation introduced in § 2.3.). Let us suppose that I is finite ; then I admits a greatest element, let us say i_0. Let $i_1=i_0+1$; for all j greater than or equal to 0, the descendance of order j of the apical cell of x_{i_1} consist of only one term : $|\gamma_j(x_{i_1}, |x_{i_1}|-1, |x_{i_1}|)|=1$. We also know that there exist p_{i_1} and q_{i_1} such that, for all j greater than or equal to p_{i_1}, we have $\gamma_j(x_{i_1}, 0, |x_{i_1}|-1) = h^{q_{i_1}}$, and therefore $|\gamma_j(x_{i_1}, 0, |x_{i_1}|-1)| = q_{i_1}$. Now, it follows from the decomposability of descendances that, for all j, we have

$$|x_{i_1+j}| = |(\delta')^j(x_{i_1})| = |\gamma_j(x_{i_1}, 0, |x_{i_1}|-1)| + |\gamma_j(x_{i_1}, |x_{i_1}|-1, |x_{i_1}|)|$$

and then, for all j greater than or equal to p_{i_1}, $f_{S_a}(i_1+j) = |x_{i_1+j}| = q_{i_1}+1$, which is inconsistent with the hypothesis (P 2.1) on infinite growth.

3.1.3. *The apical cell is never in the stationary state*

This is a direct consequence of § 3.1.2. (effectively, once in the stationary state, the apical cell will never divide again).

3.1.4. *For i sufficiently great, x_i comprises an initial stationary section of which length tends to infinity with i*

For all i, let r_i ($\geqslant 0$) be the greatest integer such that the section of x_i delimited by 0 and r_i is stationary; i.e. $T(x_i, 0, r_i) = h^{r_i}$ and $T(x_i, r_i, r_i+1) \neq h$ (we note that, the apical cell never being in the state h, we have $r_i < |x_i|$). It follows from the stationarity of h that, for any integer p ($\geqslant 0$), we obtain, $\gamma_p(x_i, 0, r_i) = T(x_{i+p}, 0, r_i) = h^{r_i}$, and therefore $r_{i+p} \geqslant r_i$; the sequence with r_i for its general term is therefore increasing (i.e., if $i' \geqslant i$, then $r_{i'} \geqslant r_i$). In order to show that r_i tends to infinity with i, we are going to establish that, for all integers i ($\geqslant 0$), there exists i', strictly greater than i, such that $r_{i'} > r_i$. Thus, let i be fixed, and let i'' be an integer, strictly greater than i, for which the length of the filament has just increased (that is, $|x_{i''-1}| < |x_{i''}|$); such an i'' necessarily exists by virtue of the hypothesis of infinite growth. Then we distinguish between two cases: either

(i) $r_{i''} = |x_{i''}|-1$ (i.e. $x_{i''}$ deprived of its apical cell is a stationary filament), then $r_{i''} \geqslant |x_{i''-1}| > r_{i''-1} \geqslant r_i$, or

(ii) $r_{i''} < |x_{i''}|-1$. Let $j = r_{i''}+1$; $T(x_{i''}, j-1, j)$ is the first term of $x_{i''}$ non-equal to h, and we know that (using the notation of § 3.1.1.) $\gamma_{p_{i''j}}(x_{i''}, j-1, j) = h^{q_{i''j}}$; then it follows that

$$\begin{aligned} T(x_{i''+p_{i''j}}, 0, r_{i''}+q_{i''j}) &= T(x_{i''+p_{i''j}}, 0, r_{i''})\, T(x_{i''+p_{i''j}}, r_{i''}, r_{i''+q_{i''j}}) \\ &= h^{r_{i''}} \gamma_{p_{i''j}}(x_{i''}, j-1, j) = h^{r_{i''}+q_{i''j}} \end{aligned}$$

therefore

$$r_{i''+p_{i''j}} \geqslant r_{i''}+q_{i''j} > r_{i''} \geqslant r_i$$

Thus, the stated property is well satisfied, with i' equal to i'' in one case, and to $i''+p_{i''j}$ in the other.

3.1.5. *Minimal expression of the property (P 2.2): stationary outcome*

We are going to establish that (P 2.2) is equivalent to the following property:

(P 2.2′) There exists p such that the descendance of order p of the section of the axiom x_0 delimited by 0 and $|x_0|-1$ is stationary; for all i, such that, in the transition from $i-1$ to i, the apical cell divides (i.e. $|\gamma(x_{i-1}, |x_{i-1}|-1, |x_{i-1}|)| = 2$), there exists p' such that the descendance of order p' of the *sub-apical* cell of x_i (i.e. $\gamma_{p'}(x_i, |x_i|-2, |x_i|-1)$) is stationary.

It is clear that (P 2.2) implies (P 2.2′). Conversely, let us suppose that (P 2.2′) is satisfied and let us prove, by induction on i, that, for all i, the descendance of a sufficiently high order of $T(x_i, 0, |x_i|-1)$ is stationary. The first part of (P 2.2′) expresses this property for $i=0$. Let us suppose that it is satisfied for $i-1$; then two cases may occur:

(i) At step $i-1$, the apical cell does not divide; then for all p, $\gamma_p(x_i, 0, |x_i|-1) = \gamma_{p+1}(x_{i-1}, 0, |x_{i-1}|-1)$ and the property is obvious.

(ii) At step $i-1$, the apical cell divides; then, for all p, $\gamma_p(x_i, 0, |x_i|-2) = \gamma_{p+1}(x_{i-1}, 0, |x_{i-1}|-1)$; furthermore, it follows from the property of decomposability of descendances that, $\gamma_p(x_i, 0, |x_i|-1) = \gamma_p(x_i, 0, |x_i|-2)\gamma_p(x_i, |x_i|-2, |x_i|-1)$; therefore $\gamma_p(x_i, 0, |x_i|-1)$ is the product, with respect to the concatenation, of two filaments which are both stationary for sufficiently high values of p.

3.2. *Growth function of some special S_a systems*

For all i, let x_i' be the ‘ final non-stationary section ’ of x_i; that is to say, with the notation introduced in § 3.1.4., we have $x_i = h^{r_i} x_i'$. This section x_i' is not empty, because the apical cell is never in the stationary state h; we are going to look for the form of the growth function associated with two particular cases of S_a systems.

3.2.1. *Particular case of S_a systems with a stationary outcome bounded in time*

We consider here S_a systems which satisfy the following property (using the notation introduced in § 3.1.1.):

(P 3) There exists a strictly positive integer M, such that, for all i, $p_i \leqslant M$; (it follows from the equality $p_i = \sup(p_{i1}, \dots, p_{i,|x_i|-1})$ that $p_i \leqslant M$ is equivalent to: for all j, such that $1 \leqslant j \leqslant |x_i|-1$, $p_{ij} \leqslant M$).

S_a systems which possess the property (P 3) are termed $S_{a'}$ systems.

(*a*) Let us prove that, for such a system, we have: for any $i \geqslant M$, $|x_i'| \leqslant 2^M$. (We are actually going to prove that, for all i, we have $|x'_{i+M}| \leqslant 2^M$.) Effectively, it follows from the property of decomposability of descendances, that:

$$\begin{aligned} x_{i+M} = (\delta')^M(x_i) &= \gamma_M(x_i, 0, |x_i|-1)\gamma_M(x_i, |x_i|-1, |x_i|) \\ &= h^{q_i}\gamma_M(x_i, |x_i|-1, |x_i|) \end{aligned}$$

therefore, we obtain $|x'_{i+M}| \leqslant |\gamma_M(x_i, |x_i|-1, |x_i|)|$; now, the descendance of order M of a section of length 1 is, according to (P 1.1), of maximum length 2^M. Therefore, we obtain $|x'_{i+M}| \leqslant 2^M$.

(*b*) Form of the growth function.

Let us first note that if two filaments v_1 and v_2 are such that $v_1 = h^{s_1}w$ and $v_2 = h^{s_2}w$, with s_1 and s_2 greater than or equal to m, then, $T(\bar{v}_1, s_1+i-1, s_1+m+n+i)$ and $T(\bar{v}_2, s_2+i-1, s_2+m+n+i)$ coincide for all i such that $1 \leqslant i \leqslant |w|$ (where $\bar{v}_1$ and $\bar{v}_2$ are the extensions of v_1 and v_2 defined in § 2.2.). Now we have

$$\gamma_1(v_1, |v_1|-|w|, |v_1|) = \prod_{1 \leqslant i \leqslant |w|} \delta(T(\bar{v}_1, s_1+i-1, s_1+m+n+i))$$

and likewise

$$\gamma_1(v_2, |v_2|-|w|, |v_2|) = \prod_{1 \leqslant i \leqslant |w|} \delta(T(\bar{v}_2, s_2+i-1, s_2+m+n+i))$$

Therefore,

$$\gamma_1(v_1, |v_1| - |w|, |v_1|) = \gamma_1(v_2, |v_2| - |w|, |v_2|)$$

Let us denote by $w^{(1)}$ this last sequence; it follows that

$$\delta'(v_1) = h^{s_1} w^{(1)} \text{ and } \delta'(v_2) = h^{s_2} w^{(1)}$$

Thus, we prove by induction that, for all l, there exists $w^{(l)}$ such that,

$$(\delta')^l(v_1) = h^{s_1} w^{(l)} \text{ and } (\delta')^l(v_2) = h^{s_2} w^{(l)}$$

Then we note that, since the alphabet A is finite, there is only a finite number of filaments of length lower than or equal to 2^M; then it follows from § 3.1.4. and § 3.2.1. (*a*) that we can find two integers, i_0 and i_1, satisfying

$i_1 > i_0$ (let us call p the difference $i_1 - i_0$);
$i_0 \geqslant M$;
$r_{i_1} > r_{i_0} \geqslant m$ (let us note that $s = r_{i_1} - r_{i_0}$);
$x'_{i_1} = x'_{i_0}$ (let us call this sequence w).

Therefore we have $x_{i_0} = h^{r_{i_0}} w$ and $x_{i_0+p} = h^{r_{i_0}+s} w$, and then there exists $w^{(p)}$ such that $(\delta')^p(x_{i_0}) = h^{r_{i_0}} w^{(p)}$ and $(\delta')^p(x_{i_0+p}) = h^{r_{i_0}+s} w^{(p)}$; in particular, we have $w^{(0)} = w$. Now, $(\delta')^p(x_{i_0}) = x_{i_0+p} = h^{r_{i_0}+s} w$; therefore, $w^{(p)} = h^s w$, and it follows that: $x_{i_0+2p} = (\delta')^p(x_{i_0+p}) = h^{r_{i_0}+2s} w$. Thus we prove by induction that, for any integer k, we have

$$x_{i_0+kp} = h^{r_{i_0}+ks} w$$

and, for all l, such that $0 \leqslant l < p$,

$$x_{i_0+kp+l} = h^{r_{i_0}+ks} w^{(l)}$$

Therefore,

$$f_{S_{a'}}(i_0 + kp) = |x_{i_0+kp}| = |w| + r_{i_0} + ks$$

and, if $0 \leqslant l < p$, $f_{S_{a'}}(i_0 + kp + l) = |w^{(l)}| + r_{i_0} + ks$. In other words, we have, for any $n \geqslant i_0$, $f_{S_{a'}}(n) = (s/p)n + (r_{i_0} - (s/p)i_0 + |w^{(\dot{n})}|)$, where $\dot{n}$ denotes the class of congruence of $n - i_0$, modulo p (i.e. $\dot{n}$ is the unique integer such that $0 \leqslant \dot{n} < p$, and $n - i_0 - \dot{n}$ is a multiple of p).

Thus, a one-dimensional array of cells, of which the type of development is assumed to fall under the class of PD(m, n)L systems of type $S_{a'}$, will have, from some stage of development onward, a growth function equal to the sum of a *linear* function with a strictly positive slope, and a *periodic* function.

3.2.2. *Particular case of S_a-systems without influence of context on the right*

We consider here PD$(m, 0)$L systems of type S_a (not necessarily satisfying (P 3)); such systems are called $S_{a''}$ systems.

(*a*) We are going to prove that, after a certain time step, two distinct steps for which the first non-stationary element is the same, have necessarily initial stationary sections of distinct lengths.

To prove that, let us suppose that there exist i_0 and i_1 (distinct) such that x_{i_0} and x_{i_1} both have the same initial section of length $r+1$, namely $h^r a$ where $a \neq h$ (therefore $r_{i_0} = r_{i_1} = r$, and we assume that $r \geqslant m$). Since the sequence with r_i

for its general term is increasing, we have necessarily, for all i such that $i_0 \leqslant i \leqslant i_1$, $r_i = r$ (and then, in particular, $r_{i_0+1} = r$). Moreover, r being greater than or equal to m, and n being equal to 0, we obtain $T(\bar{x}_{i_0}, r, r+1+m) = T(\bar{x}_{i_1}, r, r+1+m) = h^m a$ and then, $\gamma(x_{i_0}, r, r+1) = \gamma(x_{i_1}, r, r+1)$. This common filament (of length 1 or 2) has, since $r_{i_0+1} = r$, a first element distinct from h; let us denote it by a'; x_{i_0+1} and x_{i_1+1} have therefore the same initial section of length $r+1$, namely $h^r a'$ and in particular, $r_{i_1+1} = r$. Thus we prove by induction that after the step i_0, the sequence with r_i for its general term would be constant, which is impossible.

(b) The alphabet A is finite; let K be the number of its elements. Therefore, if i' and i'' are two steps the difference of which is greater than or equal to $K-1$, there exists, at least, a pair (i_0, i_1) such that $i' \leqslant i_0 < i_1 \leqslant i''$, for which the first non-stationary elements are the same; then it follows from § 3.2.2. (a) that if $r_{i'} \geqslant m$, we have $r_{i_1} > r_{i_0}$, and then, *a fortiori*, $r_{i''} > r_{i'}$.

Therefore the sequence with r_i for its general term admits as its lower bound an affine function $(x \to \alpha x + \beta)$ with a strictly positive slope (actually, we can take $\alpha = 1/K-1$); the same holds true with respect to the function $f_{S_{a''}}$. (Let us note that if the sequence with $|x_i'|$ as its general term should be bounded, we should again have the situation of § 3.2.1., that $f_{S_{a''}}$ is the sum of a linear function and a periodic function.)

Thus a one-dimensional array of cells, of which the type of development is assumed to fall under the class $(S_{a''})$ of PD$(m, 0)$L systems of type S_a, will have a growth function which admits as its lower bound an affine function with a strictly positive slope.

4. Concluding remarks

Two results have been obtained with regard to the growth function associated with two particular cases of L systems of type S_a. The result dealing with systems of type $S_{a''}$ is essentially of theoretical interest in the much investigated field of growth functions of L systems; in particular, it shows that a PD$(m, 0)$L system of type S_a cannot have a growth function of logarithmic type.

The result dealing with systems of type $S_{a'}$ leads to some remarks of a biological nature. We have shown that the growth function associated with systems such as $S_{a'}$ is the sum of a linear function with a strictly positive slope, and a periodic function. It is interesting to note that among all possible combinations of growth curves possessing the preceding property, many of them have necessarily the graphical aspect of growth curves with successive ' platforms ' because of the necessarily increasing nature, in a broad sense, of the growth curve and through its periodic component. This kind of growth is very typical and often encountered experimentally. The elementary model considered here therefore enables us (without losing sight of the restrictive aspect of a development only considered in a cellular array) to associate a type of growth curve often met with a frequent type of development. Furthermore, this model shows, certainly very schematically, a possible explanation of certain periodic phenomena: in fact, we have shown that in the case of systems of type $S_{a'}$, it is the finite nature of the set of discrete cellular states which originates the periodic component of the growth curve.

On the other hand, the same results might have been obtained for systems showing an analogous type of development, for instance the ones where a generating layer of cells gives respectively, on the left and on the right, two distinct tissues. Furthermore, in the case of a choice of unit not defined as the cell, the results obtained would have been unchanged if we had chosen a maximum divisibility greater than two (see (P 1.1)).

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